

DISCONTINUITY IN THE PLIO-PLEISTOCENE EURASIAN WATER VOLE LINEAGE

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ABSTRACT. A supposed lineage extending from *Mimomys occitanus* – *M. ostramosensis* to *Arvicola terrestris* through at least seven species has been widely accepted. The early part of the lineage, from *M. occitanus* to *M. ostramosensis*, has been shown mathematically to be a good example of phyletic gradualism. But the transition from *M. ostramosensis* to *M. savini* is somewhat hypothetical. A new morphological analysis of the type population of *M. savini* (West Runton, England) has demonstrated that this species cannot be derived from *M. ostramosensis*, but must stem from another parent species, possibly *M. coelodus* or *Cromeromys irtyschensis*. There are, in fact, two distinct lineages characterized by different *linea sinuosa* and occlusal morphologies, the first corresponding to *M. occitanus* – *M. ostramosensis*, and the second to *Cromeromys savini* – *A. terrestris*. Phyletic gradualism is demonstrated by a new graphic presentation of both lineages. This changed phyletic relationship has no biostratigraphical repercussions.

VOLES (Arvicolidae, Rodentia) figure abundantly in the Plio-Pleistocene fossil record (Chaline 1972, 1987). Among the 140 lineages identified for the period, the Eurasian water vole lineage is of major evolutionary and biostratigraphical interest. This lineage extends from *Mimomys occitanus* – *M. polonicus* – *M. pliocaenicus* – *M. ostramosensis* – *M. savini* to *Arvicola terrestris*. The part of the lineage that runs from *M. occitanus* to *M. ostramosensis* has been used for quantitative testing of phyletic gradualism on a European scale (Chaline and Laurin 1986; Viriot *et al.* 1990; Chaline *et al.* 1993).

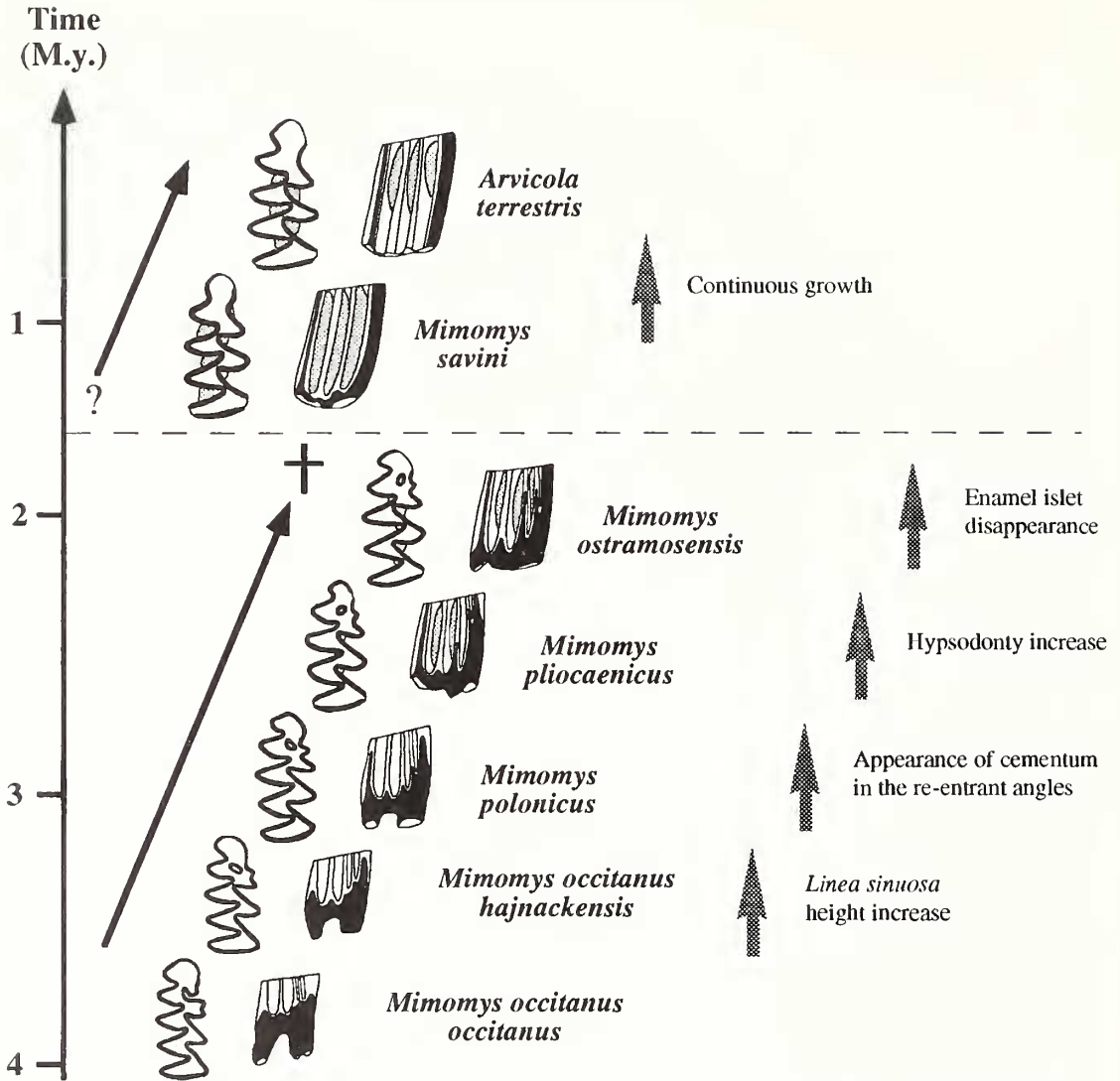
The only remaining hypothetical aspect of the lineage is the transition from *M. ostramosensis* to *M. savini* (Viriot 1989; Kolfschoten 1990*a*, 1993), in part because of the sparse fossil populations. Although the transition seemed plausible in a stratophenetic approach to the development of the lineage, no quantitative test had been made. The purpose of this paper is to carry out this quantitative test, focusing on an abundant and previously unstudied population of *Mimomys savini* from the type locality.

MATERIAL

To test the transition between the *Mimomys occitanus* – *M. ostramosensis* lineage and *M. savini*, the following species and populations have been subjected to morphometric analyses: *Mimomys occitanus occitanus* from Sète (Hérault, France); *Mimomys occitanus hajnackensis* from Wölfersheim (Germany); *Mimomys polonicus* from Rebielice Krolewski 1 and 2 (Poland); *Mimomys polonicus* from Commenailles (Bresse Valley, France); *Mimomys ostramosensis* from Montoussé 5 (Pyrenees, France); *Mimomys savini* from West Runton, Upper Freshwater Bed (England); *Mimomys savini* from Kortchevo (Russia).

THE *M. OCCITANUS* – *M. OSTRAMOSENSIS* CHRONOMORPHOCLINE

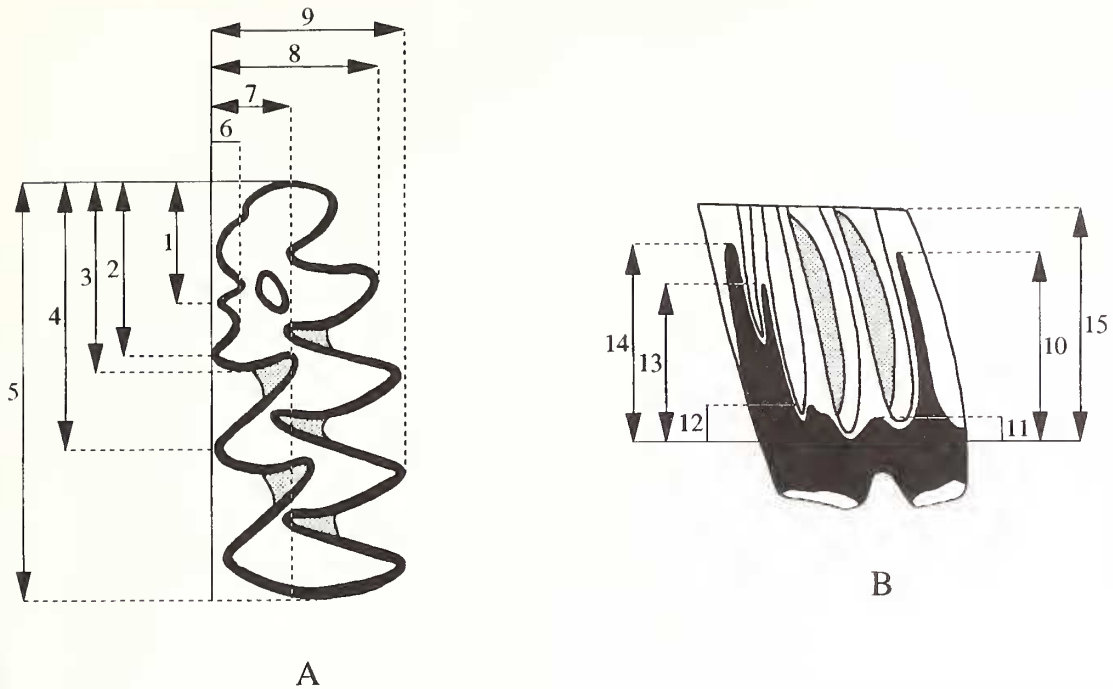
The water vole lineage (Text-fig. 1) was progressively pieced together as new fossil populations were discovered (Hinton 1926; Heim de Balsac and Guislain 1955; Chaline and Michaux 1969, 1974, 1975; Kretzoi 1969; Chaline 1974, 1984; Janossy and Meulen 1975). The first species to be described



TEXT-FIG. 1. Phyletic gradualism in the *Mimomys occitanus* - *M. ostromosensis* lineage, showing the major evolutionary trends: increased hypsodonty related to a higher *linea sinuosa*; appearance of cementum in the re-entrant angles, and disappearance of the enamel islet. Continuous growth only occurs between *Mimomys savini* and *Arvicola terrestris cantiana* (after Chaline 1987, modified).

was *M. pliocaenicus* (Forsyth Major 1902) from Castelfranco in Italy, followed by *M. savini* (Hinton 1926) from West Runton in England and *M. stehlini* (Kormos 1931). The lineage was completed by the description of *M. occitanus* (Thaler 1955), *M. polonicus* (Kowalski 1960), and *M. silasensis* (Janossy 1974), which was shown to be synonymous with *M. occitanus* by Chaline and Laurin (1986). Janossy and Meulen (1975) described an evolved stage of *M. pliocaenicus* under the name of *M. ostromosensis*. Finally, Weerd (1978) rounded off the lineage by describing a primitive *M. occitanus* as *M. davakosi*.

Quantitative analysis, restricted to the *M. occitanus* - *M. ostromosensis* part of the lineage, using morphometric methods (Chaline and Laurin 1986) showed that evolution involved (1) morphological



TEXT-FIG. 2. Nine occlusal measurements (A) and six jugal measurements (B) of the *Mimomys* first lower molar used for multivariate analysis.

changes in the occlusal surface of the first lower molar (*Mimomys* ridge, enamel islet), (2) appearance of cementum in the re-entrant angles, and, above all, (3) a rapid, though irregular, increase in the rate of hypsodonty conveyed by the increased height of the *linea sinuosa* on the crown sides and (4) by the non-appearance of roots (Text-fig. 1). Digital image processing applied to area quantification (Viriot *et al.* 1990), likewise confined to the *M. occitanus* – *M. ostramosensis* part of the lineage, showed that while the anterior part of the occlusal surface was becoming simpler the posterior part was increasing in complexity. The lineage *M. occitanus* – *M. ostramosensis* is a chronomorphocline that stretches from Western Europe (Spain and England) to Siberia and even China (Zheng and Li 1986; unpublished observations by Chaline at the Beijing Institute of Palaeontology and Palaeoanthropology). This vast range means that the lineage is a yardstick in Eurasia for establishing a high-resolution biostratigraphy of the Pliocene and Lower Pleistocene (Chaline 1989; Chaline and Farjanel 1990).

THE *MIMOMYS SAVINI* – *ARVICOLA TERRESTRIS* LINEAGE

Hinton (1926) first suggested the transition from *M. savini* to *Arvicola*. The gradual transition from *M. savini* to *A. terrestris cantiana* and thence to *A. terrestris terrestris* has likewise been demonstrated (Heim de Balsac and Guislain 1955; Koenigswald 1980; Kolfshoten 1990a, 1990b). Zazhigin (1980) described *M. intermedius* (= *M. savini*) under a new genus *Cromeromys*, created for the Siberian species *irtyshensis*.

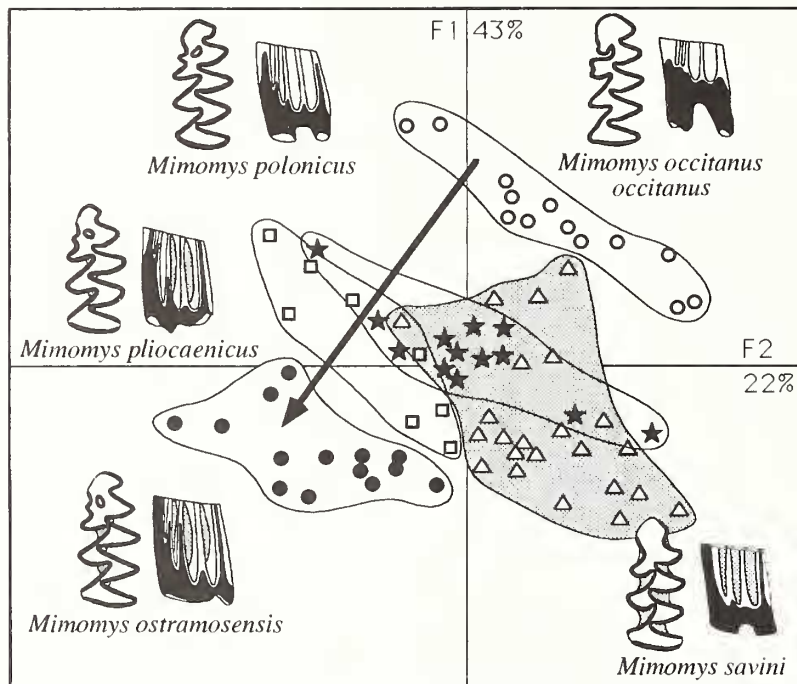
Quantitative studies of the *A. terrestris cantiana* – *A. terrestris terrestris* lineage showed a relative variation in the thickness of the anterior and posterior walls of the tooth triangles (Koenigswald 1980; Heinrich 1982; Kolfshoten 1990a, 1990b, 1992). When converted into index form, this gradual change found an application in quantitative biostratigraphy. Although the evolution is

gradual, it is not always linear, at least not in north-western Europe. The thickness index displays a clinal variation from north to south across Europe, and southern populations have a more primitive appearance with a lower index (Röttger 1986). Where advanced populations became extinct in the north during the late Middle Pleistocene, they were replaced by more primitive populations which migrated from southern areas thus altering the progressive variation over time by a reversal in the thickness index (Kolfshoten 1990a, 1992).

A NEW POPULATION ANALYSIS OF *MIMOMYS SAVINI*

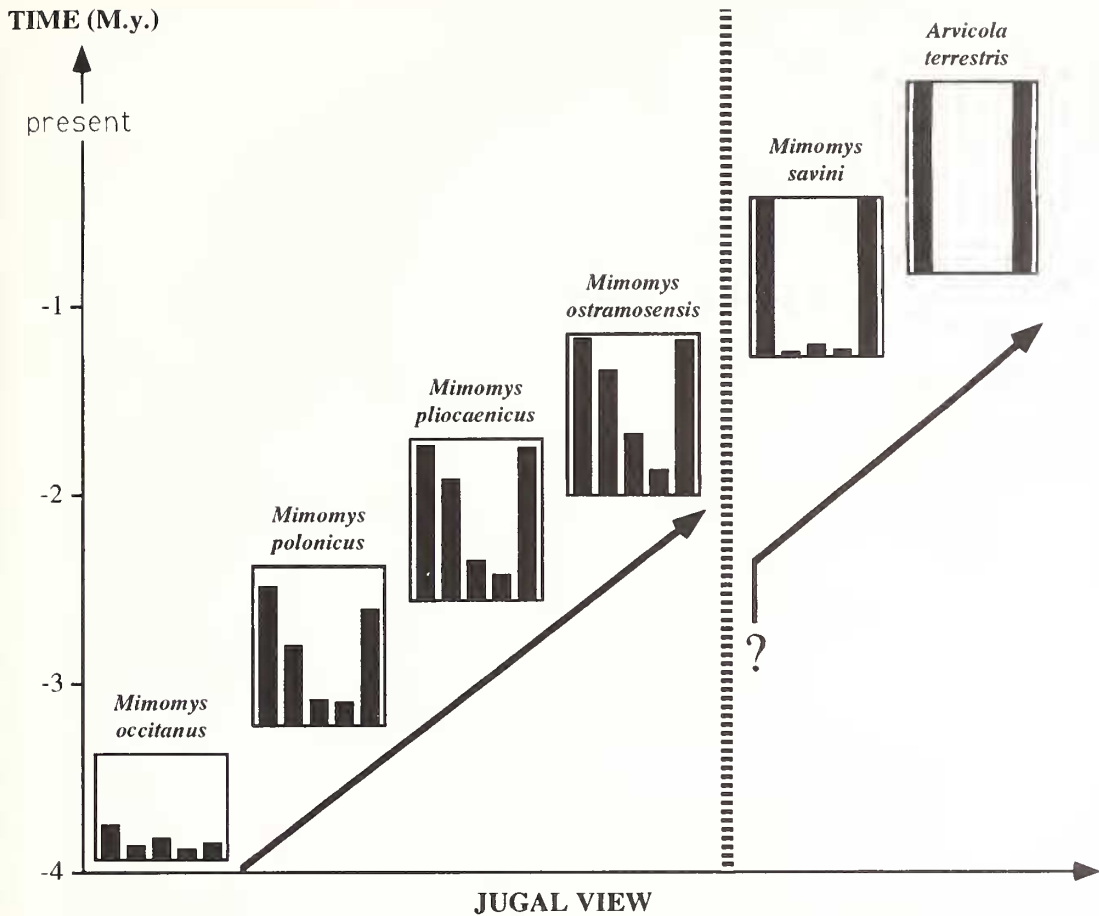
A bivariate study of variability in *M. savini* was conducted independently of the remainder of the lineage (Pasquier 1972). This species supposedly formed a transition with the *Arvicola* genus but had never figured in a general quantified analysis. Analysis of a fairly abundant, previously unstudied population from the type locality of the Freshwater Bed, West Runton, England) provides insight into the question.

A new multivariate analysis was performed using the classic biometric parameters (Text-fig. 2). It clearly shows that there is a trend from *M. occitanus occitanus* to *M. ostromosensis* (Text-fig. 3), and



TEXT-FIG. 3. Multivariate analysis based on Text-figure 2 measurements. The morphological variability of *M. savini* does not fit in with that of *M. ostromosensis* as could have been expected if *M. savini* derived from *M. ostromosensis* and continued the sequence *M. occitanus* – *M. ostromosensis*. Differences concern the anterior complex morphology (parameters 1–3) and the *linea sinuosa* (especially parameters 11–13). There is a clear discontinuity between the two lineages (○, *M. occitanus occitanus*; ★, *M. polonicus*; □, *M. pliocaenicus*; ●, *M. ostromosensis*; △, *M. savini*).

that the morphological variability of *M. savini* (none occlusal and six lateral characters) does not fit in with that of *M. ostromosensis* as could have been expected if *M. savini* were descended from *M. ostromosensis*.



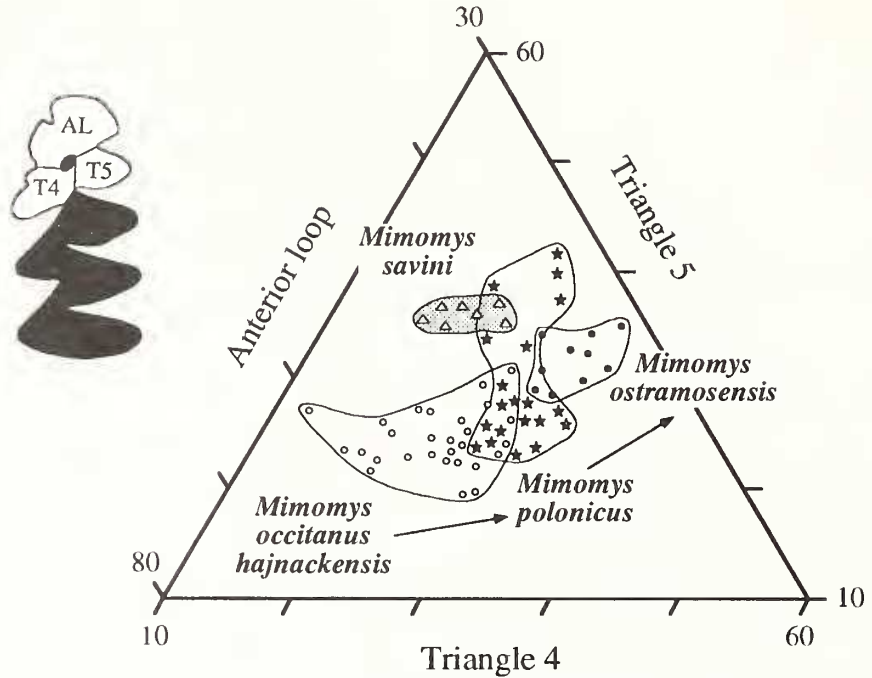
TEXT-FIG. 4. *Linea sinuosa* changes in the *M. occitanus* – *M. ostramosensis* lineage compared with the *M. savini* – *A. terrestris cantiana* sequence. The jugal views correspond to mean values of populations calculated for each species for parameters 10–15. It is clear that the gradual evolution of the *linea sinuosa* in *M. occitanus* – *M. ostramosensis* does not continue in *M. savini*. There is a discontinuity suggesting that *M. savini* derives from another *Mimomys* lineage, perhaps from *M. coelodus*.

The *linea sinuosa* variations observed in jugal view (Text-fig. 4) show that the pattern of change from *M. occitanus* to *M. ostramosensis* involves a distinct upturn of folds 1 and 5 towards the top of the crown and a more limited upward extension of folds 2, 3 and 4 which recede from front to back. This is obviously a gradual evolution.

When these data are compared with *M. savini*, however, a major difference can be seen in the pattern of the *linea sinuosa*. While folds 1 and 5 rise towards the top of the crown, folds 2, 3 and 4 remain very low. *M. savini* does not derive from *M. ostramosensis* but probably from another *Mimomys* lineage.

The occlusal morphology of the anterior complex of *M. occitanus hajnachensis*, *M. polonicus*, *M. ostramosensis* and *M. savini* has been quantified by digital image processing. This computerized technique describes the geometry of objects in a bidimensional space (for details, see Viriot 1989, Viriot *et al.* 1990 and Viriot *et al.* 1993). It is well understood that, in the course of M_1 occlusal evolution in the Eurasian water vole lineage, the greatest changes took place in the anterior

complex. This anterior complex can be broken down into three parts: triangle 4, triangle 5 and the anterior loop. The percentage of the area occupied by these three parts with regard to the total area of the anterior complex can be quantified (Text-fig. 5). From *M. occitanus hajnackensis* to *M.*



TEXT-FIG. 5. Evolutionary trends in the anterior complex of the M_1 from *M. occitanus* to *M. savini* described by digital image processing. Overlapping clouds from *M. occitanus hajnackensis* to *M. ostramosensis* characterized by a decrease in the area occupied by the anterior loop to the profit of triangles 4 and 5. Discontinuity of the *M. savini* plot with an increased area of the anterior loop at the expense of triangle 4 (○, *M. occitanus hajnackensis*; ★, *M. polonicus*; ●, *M. ostramosensis*; △, *M. savini*).

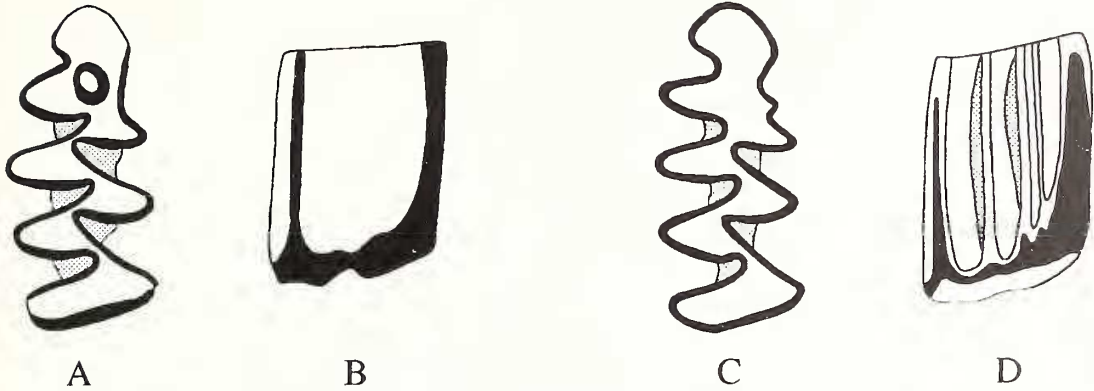
ostramosensis, the area occupied by the anterior loop decreases gradually to the profit of both triangles 4 and 5. Then, if we look at the passage from *M. ostramosensis* to *M. savini*, the process is reversed and the area occupied by the anterior loop increases at the expense of triangle 4 alone. There is a clear discontinuity between the *Mimomys* part of the lineage and the *Arvicola* part, which includes *M. savini*.

THE POSSIBLE ORIGIN OF THE SAVINI LINEAGE

According to the present knowledge of *Mimomys* species, two possible origins can be attributed to the *savini* lineage.

First, Rabeder (1981, text-fig. 81-2b), noticed that the *linea sinuosa* of *Mimomys coelodus* displays only a minor upturn of fold 2 as in some *M. savini*. Moreover, in Zazhigin's figures (Zazhigin's 1980, text-figs 25-8, 9), the *linea sinuosa* of *M. coelodus* has small upturns of the three intermediate folds

as in other *M. savini*. Finally, according to Kretzoi (1954), the holotype of *M. coelodus* coming from the Kislang fauna (Hungary), is closely related to *M. intermedius*, a species previously synonymized with *M. savini*. Therefore, *M. coelodus* is a species with hypsodont molars, with a M_1 displaying a well-developed enamel islet and no *Mimomys* ridge (Text-fig. 6A–B). Therefore, *M. coelodus* is a



TEXT-FIG. 6. Holotypes: A–B, *M. coelodus*; A, occlusal view; B, jugal view (after Rabeder 1981). C–D, *C. irtyshensis*; C, occlusal view; D, jugal view (after Zazhigin 1980).

possible ancestor of *M. savini*. However, the relationship between *M. coelodus* and the larger late Biharian voles has not yet been investigated properly and remains hypothetical, while the taxonomic status of *M. coelodus* is unknown.

The second hypothesis corresponds to Zazhigin's opinion, that *M. savini* should be regarded as part of the *Cromeromys* lineage, known from Late Pliocene deposits from Western Siberia and Transbaikalia, and from Early and Middle Pleistocene deposits from Eurasia. Indeed, the *linea sinuosa* of *Cromeromys irtyshensis*, the type species (Zazhigin 1980, fig. 24-1-8), looks very much like those of *M. coelodus* and *M. savini* (Text-fig. 6C–D). Moreover, the larger voles from West Runton, referred to as *C. intermedius* and related to *C. irtyshensis*, are often assigned to *M. savini* (Kretzoi 1969, Zazhigin 1980), according to their characteristic M^3 .

As *M. savini* can no longer be placed within the lineage of the genus *Mimomys* (type species *Mimomys pliocaenicus*), it must be assigned to *Cromeromys savini* (Hinton, 1910).

In summary, the discontinuity between the lineages *M. occitanus* – *M. ostramosensis* and *C. savini* – *A. terrestris* implies that the first lineage, which displays gradual morphological evolution, ends with *M. ostramosensis*. The lineage is replaced stratigraphically and, it seems, ecologically by that of *C. savini*, which is of uncertain origin, which gradually leads to *A. terrestris cantiana* and which continues to the present day with *A. terrestris terrestris*. This discontinuity between the two lineages was masked by the fact that *C. savini* succeeds *M. ostramosensis* in the same stratigraphical sequences. The phylogenetic re-arrangements introduced here do not change the biostratigraphical significance of *C. savini*.

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